A redefinition of *Pseudokellya* Pelseneer, 1903 (Bivalvia: Cyamiidae) and the description of a new species from the Southern Ocean

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ABSTRACT

A new species of *Pscudokellya*, *Pscudokellya franki* from South Shetland Islands, is described. *P. franki* is characterized by its subcircular shell outline, the periostracum forming low lamellate commarginal folds, radial sculpture absent, and by the presence of a single posterior siphonal opening, a fact that is in contrast with that reported for the type species of *Pscudokellya*, *Kellia cardiformis* Smith, 1885. The presence of a complete follicle surrounding each developing oocyte, persisting throughout vitellogenesis, a condition not currently known for other bivalves, is confirmed as a generic diagnostic character. The generic redefinition, based on shell morphology and anatomical features described for *Pseudokellya franki*, is given.

Additional Keywords: Cyamioidea, *Cyamiocardium, Kellia, Perrierina*, reproduction

INTRODUCTION

Pseudokellya was proposed by Pclscneer (1903) to reallocate Kellia eardiformis Smith, 1885, a species described from Kerguelen Islands. The diagnosis for the new genus was given in association with description of the anatomy of Kellia eardiformis. Species of Pseudokellya were originally distinguished from those of Kellia Turton, 1822, by having two, branchial and anal, siphonal openings and for being dioecious. Pelseneer (1903) also reported a peculiar reproductive trait for *Pseudokellya* eardiformis: the presence of a complete follicular epithelium surrounding each developing oocyte, a condition not otherwise known for bivalves. Subsequently, four nominal species of *Pseudokellya* were described: *Pseudo*kellya gradata Thiele, 1912, from Gauss Station, Pseudokellya stillwelli Hedley, 1916, from Adelie Land and Davis Sea (a synonym of *P. eardiformis*, according to Dell (1990)), Pseudokellya georgiana Dell, 1964, from South Georgia, and Pseudokellya inexpectata Dell, 1964, from South Georgia and South Orkneys. The descriptions of these four species were based exclusively on shell

characters; after that not a single study provided information on their anatomy. Consequently, to date, it is not possible to confirm if the anatomical characters reported by Pelseneer (1903) are diagnostic for *Pseudokellya eardiformis* or shared by other species of the genus.

In the present paper, a new species of *Pseudokellya* from South Shetland Islands is described; details on anatomy, reproductive traits and shell morphology provide additional information for a better definition of the genus.

MATERIALS AND METHODS

The specimens studied were originally deposited at the Zoologisches Museum (ZMB), Germany. They were collected during the 1982, 1985, and 1986 Soviet Antarctic Expeditions to King George Island, South Shetland Archipelago. Voucher specimens arc deposited at the ZMB, Museo de La Plata (MLP), and Museo Argentino de Ciencias Naturales (MACN), Argentina.

We studied the holotype of *P. gradata* (ZMB 63109), specimens of *P. eardiformis* (ZMB 63136), *P. inexpectata* (ZMB 114683), and *P. georgiana* (MLP 12999) from type localities, and specimens of *P. gradata* from Zoologische Staatssammlung Münich (ZSM), Germany (ZSM 20012865: 63° 01.10′ S, 61° 09.10′ W; ZSM 20041320: 62° 00.09′ S, 60° 19.31′ W). Specimens currently assigned to *Kellia suborbieularis* (Montagu, 1803) (MLP 11563); *Kellia magellaniea* Smith, 18S1 (MLP 13000); and *Kellia* sp. (MLP 13001) from Argentine waters were also used for comparative purposes.

The anatomical description of *Pseudokellya franki* was based on dissections under stereoscopic microscope; seven specimens were processed for histology, inclusion was performed either in Paraplast[®] or Historesin[®]; specimens were completely sectioned at 5 µm thick, using a Leica RM 2355 microtome.

Shell morphology was studied through scanning electron microscopy (SEM). Shell measurements were

obtained according to the following criteria: L: maximum antero-posterior distance; H: maximum dorsoventral distance perpendicular to L; W: maximum distance across valves. Mean value and standard deviation for the ratios H/L and W/H are given (n = 16 specimens). Hinge teeth nomenclature is indicated in figures 10 and 11.

SYSTEMATICS

Pseudokellya Pclseneer, 1903

Type Species: *Kellya cardiformis* Smith, 1885 (by monotypy)

Pseudokellya franki new species (Figures 1–26)

Diagnosis: Shell subcircular, inflated, only sculptured with marked growth lines; periostracum forming lamellate commarginal folds. Posterior portion of the right cardinal tooth (**C3b**) well developed. A single posterior siphonal opening, the anal, present.

Description: Shell small, maximum observed L = 4.2mm, shell outline subcircular, slightly longer than high (H/L = 0.94 ± 0.04), inflated (W/H = 0.74 ± 0.04) (Figures 2-5, 12). Anterior margin short and round, imperceptibly connected with dorsal margin, forming a wide curve with the anterior part of ventral margin (Figures 2–5). Ventral margin markedly curved. Posterior margin rounded, nearly vertical in larger specimens following the posteroventral curve (Figures 2-4). Posterior part of dorsal margin suberect or slightly curved. Beaks prosogyrous, inflated, globose at tip, strongly discernible above dorsal margin, slightly displaced anteriorly (Figure 2-5, 7). Prodissoconch ovate, about 400 µm in diameter, surface sculptured with minute granules (Figures 6, 13). Shell surface whitish, shiny, with very low and rounded commarginal growth lines, irregularly distributed (Figure 15). Periostracum translucent, forming low lamellate periostracal folds (Figure 14). Inner shell surface whitish, dull. Hinge plate narrow, somewhat enlarged anterior to beaks, just at the point of insertion of cardinal teeth (Figures 8–11). Hinge: left valve (Figures 8, 10): cardinal tooth 2 (C2) solid, triangular, cusp subcentral; cardinal tooth 4 (C4) relatively short, straight, and solid, with cusp displaced posteriorly; lateral posterior tooth (LII) long, narrow, and low, well separated from posterior margin. Right valve (Figures 9, 11): cardinal tooth (C3) hook-like, formed by large, solid anterior portion (C3a), bifid at base, and short and narrow posterior portion (C3b). In



Figure 1. Location of the type locality of *Pseudokellya franki* new species.

larger specimens, **C3a** and **C3b** form a nearly right angle (Figure 11), whereas in smaller ones the angle between **C3a** and **C3b** is more acute and **C3b** longer (Figure 9). Right inner posterior lateral tooth (**L1**) long, moderately solid, with centrally located cusp; outer posterior lateral tooth (**L11**) merged with dorsal shell margin. Internal ligament set in a small, short, shallow resilifer posterior to cardinal teeth; external ligament short, posterior to beaks. Scars of anterior and posterior adductor muscles ovate, the anterior, slightly longer (Figure 7). Pallial line entire.

Anatomy: Mantle margin largely unfused, forming a long pedal gape (Figure 20), fused at the posterior quarter, delimiting the anal opening; below this point, an enlarged portion of the middle mantle fold corresponds to the position of the absent branchial mantle opening (Figure 19). The anal opening and the enlarged portion of the mantle margin are flanked by a row of 12 to 16 micropapillate tentacles on each side, placed in an alternating pattern (Figures 18, 19). Anterior and posterior adductor muscles almost equal in size, the posterior one ovate in section, the anterior more elongated and narrowcr (Figure 16). Foot long, with a well differentiated heel (Figure 16); a small byssal gland, functional

Figures 2–15. *Pseudokellya franki* new species. Specimens from Maxwell Bay, King George Island, 100 m (station 30/49). **3**, **4**. Holotype, **2**, **5–15.** Other specimens. **2–5.** Outer view, **2**, **3**. Right valve. **4**. Left valve. **5**. Juvenile. **6**. Prodissoeoneh. **7**. Inner view, left valve. **8–11**. Details of hinge plate. **8**, **9**. Specimen 4.2 mm L. **10**, **11**. Specimen 5.5 mm L. **8**, **10**. Left valve. **9**, **11**. Right valve. **12**. Dorsal view. **13**. Detail of prodissoconch sculpture. **14**. Periostraeal folds. **15**. Periostraeal folds and growth lines. Seale bars: 2-4, 7 = 1 mm; 5 = 250 µm; 6 = 100 µm; 8-11 = 200 µm; 12 = 500 µm; 13 = 25 µm; 14 = 100 µm; 15 = 50 µm. Abbreviations: **C2**, **C3a**, **C3b**, **C4** = cardinal teeth; **L1–LIII** = lateral teeth I–III; **ilig** = internal ligament; **elig** = external ligament.

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Figures 16–20. *Pseudokellya franki:* anatomy. **16.** Gross anatomy from the right side. **17–20.** Transverse sections showing details of demibranch fusion and mantle border. **17.** Posterior fusion of the inner demibranchs. **18.** Detail of mantle folds and tentacle. **19.** Fusion of posterior portion of the mantle border. **20.** Anterior portion of the mantle border. Scale bars: 16 = 1 mm; 17, 19, 20 = 300 µm; 18 = 150 µm. Abbreviations: **aam** = anterior adductor muscle; **al** = ascending lamella of inner demibranch; **bf** = branchial fusion; **dl** = descending lamella of inner demibranch; **e** = cmbryo; **f** = foot; **id** = inner demibranch; **imf** = inner mantle fold; **h** = heel; **mb** = mantle border; **mmf** = middle mantle fold; **od** = outer demibranch; **omf** = outer mantle fold; **pam** = posterior adductor muscle; **t** = tentacle.

in adults, present; byssus comprising a single, long filament. Outer and inner demibranehs present, with well-developed ascending and descending lamellae (Figure 16). Height of outer demibraneh representing onethird the height of inner one; posterior end of outer demibraneh fused to the mantle; left and right inner demibranchs, also fused at posterior end, determining defining a suprabranehial chamber continuous with the anal opening (Figure 17). Length of descending lamella of outer demibraneh about a half of ascending one; filaments of ascending lamella of inner demibraneh decreasing in length toward the posterior end.



Figures 21–26. *Pseudokellya franki*: oocytes and embryos. **21–24.** Histological sections. **25, 26.** SEM photomicrographs. **21.** Previtellogenic and early vitellogenic oocytes. **22.** Vitellogenic oocyte. **23–26.** Embryos attached to the inner demibranch. Scale bars: 21, 24–26 = 100 μ m; 22 = 50 μ m; 23 = 200 μ m. Abbreviations: **aw** = acinar wall: **bf** = branchial filaments of the inner demibranch; **dg** = digestive gland; **e** = embryo; **evo** = early pre-vitellogenic oocyte; **fc** = follicle cell; **g** = gonad; **h** = heel; **ifj** = interfilamental junction; **nu** = nucleus; **pg** = pedal gap; **pvo** = pre-vitellogenic oocyte; **st** = stalk.

Reproductive Traits: *Pseudokellya franki* is dioecious, brooding its embryos within the inner demibranchs attached to the ascending filaments by short stalks (Figures 16, 23–26). The architecture of oogenesis shows a peculiar feature, consisting of the formation of a complete one-cell-thick follicle surrounding each developing oocyte, which persists to the end of vitellogenesis (Figures 21, 22, 24).

Type Locality: Maxwell Bay, 62°10–19′ S, 58°35–58′ W, King George Island, South Shetland Islands, 100 m (station 30/49).

Type Material: Holotype (ZMB 114680-a) and 10 paratypes from the type locality (five at ZMB 114680-b; three at MLP 12997; two at MACN-In 37535).

Other Material Examined: 36 specimens, Maxwell Bay, King George Island (station 30/43), 50 m (ZMB 114679); 84 specimens, Maxwell Bay, King George Island, 100 m (station 30/49) (ZMB 114680-c); 1 specimen, Maxwell Bay, King George Island, 10–15 m (station II/134) (ZMB 114682); 6 specimens, Maxwell Bay, King George Island, 40–50 m (station B 301) (ZMB 114681).

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Figures 27–38. *Pseudokellya* species. **27–29.** *P. cardiformis* (ZMB 63136). **30–32.** *P. inexpectata* (ZMB 114683). **33–35.** *P. gradata*. **33.** Specimen from 62° 00.09′ S 60° 19.31′ W (ZSM 20041320). **34, 35.** Syntype (ZMB 63109). **36–38.** *P. georgiana* (MLP 12999). **27, 30, 33, 36.** Outer view left valve, and detail of shell scupture at the right side. **28, 31, 34, 37.** Hinge plate left valve. **29, 32, 35, 38.** Hinge plate right valve. Scale bars: 27, 30, 33, 36 = 1 mm; 28, 29, 31, 32, 34, 35, 37, 38 = 500 μm.

Distribution: Only known from South Shetland Islands (Figure 1).

Etymology: The species is named after Frank Köhler, Australian Museum, Sydney, and associated with the Museum für Naturkunde, Berlin.

Remarks: In general shell outline, *Pseudokellya franki* is most similar to *Pseudokellya cardiformis* (Figures 27–29), from which it differs in having a relatively longer and more straight posterior part of dorsal margin and a ventral margin comparatively more strikingly curved. The shell outline of *P. georgiana* (Figures 36–38) differs from that of *Pseudokellya franki* in being markedly trapezoidal; *P. gradata* (Figures 33–35) and *P. inexpeetata* (Figures 30–32) have subtrapezoidal shell outlines.

The absence of radial sculpture on the outer shell surface is a distinctive character of *Pseudokellya franki* (Figures 2–5). Also distinctive in *P. franki* is the presence of widely separated and low lamellate commarginal periostracal folds (Figure 14); in other species of *Pseudokellya*, the periostracum shows densely packed and fine commarginal threads (Figures 27, 30, 33, 36). *Pseudokellya franki* shows a weak commarginal sculpture represented by low and rounded irregular ridges, which seems to originate through growth disruptions (Figure 15); in the remaining species this sculpture is less evident, being represented only by shallow growth lines (Figures 27, 30, 33, 36). In the case of *Pseudokellya gradata*, 3–4 sharp growth disruptions, described as "grades", appear (Figure 33).

The hinge of the largest specimens of *Pseudokellya franki* is similar to that of the other species of the genus, mainly differing in having a larger cardinal tooth 3b and a more solid cardinal tooth 2 with a triangular base. In the smaller specimens the cardinal 3 is arched, with **C3b** more developed.

Anatomically, *Pseudokellya franki* differs from *P. cardiformis* (the only other species in the genus for which anatomy is known) in having only one defined mantle opening, the anal, and a differentiated portion of middle mantle fold below the anal opening that seems to represent the inhalant branchial aperture (lacking only a ventral point of fusion delimiting the opening). Pelseneer (1903) reported two posterior siphonal openings in *P. cardiformis*. As it was described by Pelseneer (1903) for *P. eardiformis*, *P. franki* showed to be dioecious. Out of the seven specimens histologically studied, four were males and three females, with no signals of a possible consecutive sexuality detected.

TOWARD A BETTER DEFINITION OF *PSEUDOKELLYA*

The generic definition of *Pseudokellya* given by Pelseneer (1903) when describing *P. cardiformis* was based on three characters: the presence of two posterior (branchial and anal) siphonal openings, the dioecious condition, and a peculiar mode of oogenesis comprising the formation of a complete follicle surrounding each developing oocyte (a condition not known, at that times, for any other bivalve).

According to Thicle (1934: 858) the diagnostic characters of *Pseudokellya* are: "shell roundish or somewhat angular, uniformly bulging, with weak radial sculpture; umbo moderately elevated, situated in the center; hinge margin posterior to the ligament prolonged somewhat ridge-shaped; anterior hinge teeth of the left valve fairly long, diverging in an acute angle".

After the new information coming from the new species described here and the species described after the diagnosis by Thiele, an expanded redescription of the genus is needed.

Redescription of Pseudokellya: Shell small, shell outline subcircular to subtrapezoidal, ventral margin uniformly curved or more sharply curved at posterior half; beaks prosogyrous, subcentrally located. Prodissoconch sculptured with microscopic granules; teleoconch usually sculptured with a variable number of more or less marked radial cords, sometimes absent. Periostracum usually elevated in fine threads or low lamellate folds. Growth lines variably marked, sometimes looking like commarginal sculpture. Hinge plate narrow, enlarged anterior to beaks, just at the cardinal teeth insertion. Right valve with a hook-like cardinal tooth (C3), formed by an anterior part (C3a) varying from short and stout to long and slender, with a triangular base, bifid to a variable degree; and a smaller posterior portion (C3b), sometimes extremely reduced in size; a well-developed, elongated, narrow, and low inner posterior lateral tooth (PI), and an outer posterior lateral tooth (**PIII**) not well-separated from dorsal margin. Left valve: two cardinal teeth, the anterior (C4) running parallel to the anterior part of dorsal margin, and the posterior (C2), usually elongated and smaller, parallel or forming an acute angle with C4; a single and elongated posterior lateral tooth (PII), present. Resilifer small and shallow, located below beaks. Internal and external ligaments, present. Mantle with one or two posterior siphonal openings. Gills each composed of two demibranchs. Foot with a welldifferentiated heel, having a small byssal gland. Animals dioecious, retaining the embryos attached by short stalks to the inner demibranch filaments; a complete follicle surrounds each developing oocyte throughout vitellogenesis.

Comparison with Other Genera: When describing *Pseudokellya*, Pelseneer (1903) focused in the prescnee of two siphonal (branchial and anal) openings and the dioecious condition, in oposition to *Kellia* which is a hermaphrodite and has only one posterior siphonal opening, the anal. It is to be noted that, in contrast to that described by Pelseneer (1903) *Pseudokellya franki* shows a single posterior mantle opening. Additional characters differentiating *Kellia* from *Pseudokellya* are found in the hinge morphology: the former has a simple and triangular right cardinal tooth C3 and two left cardinal teeth (C2 and C4) arranged in a chevron pattern. Moreover, in *Kellia* both right and left posterior lateral teeth are consistently stronger than in *Psendokellya*. In addition, *Kellia* only has the internal ligament. Lastly, the radial sculpture and periostracal folds present in some species of *Pseudokellya* are absent in *Kellia*.

The hinge of *Pseudokellya* closely resembles that of *Cyamiocardium* Soot-Ryen, 1951, and *Perrierina* Bernard, 1897, two genera also occurring in the Southern Ocean. However, in the last two an additional tooth behind the cardinal **C2** (referred to as cardinal tooth 4b) appears (Lamy, 1917; Zelaya, 2008; pers.obs.). Adult specimens of *Cyamiocardium* and *Perrierina* have an always well-developed **C3b**, which is reduced in size in larger specimens of *Pseudokellya*. *Perrierina* also has tubercles anterior and posterior to the beaks resembling a taxondont hinge, a character absent in members of *Pseudokellya* (see Zelaya, 2008).

The Geographic Distribution of *Pseudokellya*: Currently known species of *Pseudokellya* are restricted to Sub-Antarctic and Antarctic waters. According to Dell (1990), *P. cardiformis* and *P. gradata* are probably circumantarctic, extending to the Scotia Arc Islands and the former, reaching Malvinas and Kerguelen Islands. The remaining three species are restricted to the Scotia Arc islands: *P. inexpectata* known from South Georgia and South Orkneys Islands (Dell, 1964), *P. georgiana* from South Georgia (Dell, 1964), and *P. franki* from South Shetland Islands (present study).

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